SEED ECOLOGY OF SEQUOIADENDRON GIGANTEUM

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Since the discovery of giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchh.) over 100 years ago, people have been concerned about "perserving these forest monarchs." Yet little is known about seed germination in nature. Many visitors to the California groves ask why there are so few young giant sequoias visible. The answers to this question are most important to the survival of the species. Since we cannot preserve indefinitely the mature trees, we must learn more about seed and seedling ecology to encourage reproduction of the species in nature. This study is one of three and is aimed at a better understanding of the reaction of seeds of the species to the environment both in nature and under laboratory conditions. The other two studies include a field inventory of the rate of reproduction, and the response of seedlings to environmental extremes.

The proper scientific name of the species and its generic designation are still controversial subjects (Buchholz, 1939; Doyle, 1945). The author prefers to use *Sequoiadendron giganteum*.

Description of the Habitat

Eighty or more groves of *S. giganteum* are located on the west slope of the central Sierra Nevada of California at elevations of 4,430–7,540 feet (Anon, 1952). A few trees grow naturally above these elevations.

The range of groves extends a distance of 250 miles from the middle fork of the American River in Placer Co. south to Deer Creek in Tulare Co. Although its natural distribution is limited, this species is planted successfully in at least 14 other countries (Stanford, 1958).

Summers in the natural range of the species are warm and dry with almost no precipitation except for occasional light thunderstorms. Most of the annual precipitation (ranging between 24.8 and 35.8 inches) falls as snow beginning in October or November and continuing through April or May. Annual snow accumulation varies from 45–185 inches.

The warmest month of the year is August when daily air temperatures may rise to 40°C, but often drop to 2°C at night. Intense summer solar radiation on exposed sites may heat the soil surface to 65°C while temperatures on shaded sites may be as much as 16°C lower.

The winters are cold; air temperatures seldom exceed 10°C during the day and sometimes drop to minus 23°C at night. The average annual frost free period is 124 days.

Mountainous terrain with deep valleys and grassy meadows characterize the range. The main rock formations are granite, schist, diorite, and andesite. Lava caps are common on the higher peaks.

Most of the groves are on unglaciated terrain but some can be found on glacial moraine. The soils are mainly shallow and rocky but include some deep sandy loams. They are weakly to moderately acid and are generally well-drained (Zinke and Crocker, 1962).

The groves are not pure stands but contain these main tree species: *Abies concolor* (Gord. & Glend.) Lindl., *Libocedrus decurrens* Torr., *Pinus jeffreyi* Grev. & Balf., *P. lambertiana* Dougl., *P. murrayana* Grev. & Balf., *P. ponderosa* Laws., *Sequoiadendron giganteum* (Lindl.) Buchh., and *Taxus brevifolia* Nutt. A checklist of plants found in and around the groves provides a more complete picture of the flora (Stagner, 1951).

Ferns, mosses, herbs, grasses, and brush are common in some groves. Continuous mats of herbaceous and low shrubby vegetation once grew in most groves, but heavy recreational use of some areas has severely reduced the ground cover (Hartesveldt, 1962).

Description, Results, and Discussion of Tests

Each germination experiment used 10 sets of 100 seeds each placed on moist filter paper in Petri dishes, unless otherwise noted. Seeds used in each of the tests came from five different areas, representing the natural range of the species. Since no significant differences occurred among sources by area, data represent averages of the five sources for each test. Light, moisture, and temperature were standardized with only one factor varying at a time as described below. The ability of the seeds to extend the radicle and free the cotyledons in 32 days served as a criterion of successful germination. In preliminary tests, the highest total germination occurred in reduced light (5,000 f.c.) at temperatures between 10° and 20°C. The tests and results are as follows:

1. Germination of Controls (20,000 seeds). Germination percent in reduced light (3,000 to 5,000 f.c. day, dark night) on moist filter paper at temperatures of 15°C ± 1°C) was used as a germination standard for all other tests. Control germination varied between 21.0 and 55.5%. Each test was compared to its companion control run of 10 sets of 100 seeds from the same seed source and year.

2. Germination and Temperatures (27,000 seeds).

A. *Fixed Temperatures.* One thousand seeds were germinated in an incubator at each of these temperatures: 5°, 10°, 20°, 30°, and 40°C (± 0.5°C) under 7,000 f.c. light day and night. At 10°C, 39.5% of the seeds germinated while at 20°C, 40.9% of the seeds germinated. All other temperatures produced germination below 39% (table 1).

B. *Fluctuating Temperatures.* One thousand seeds were placed in Petri dishes in the weather station of the Experimental Plot (used for the seedling studies) every 32 days for 3 years to test germination under natural fluctuating temperatures. When the soil was not frozen, 100 seeds sewn in cheesecloth packets were planted in soil at 2 cm depth every 32 days to check germination in the soil environment. Moisture was added to half of the seeds daily except during the winter months when soil moisture was adequate for germination. Soil and air temperature records were checked against germination. Since fixed temperatures do not occur in nature for any appreciable length of time, germination

TABLE 1. GERMINATION PERCENT OF SEED AT FIXED TEMPERATURES—5,000 SEEDS TOTAL, 500 PER TEST

	5°C	10°C	20°C	30°C	40°C
Percent germination	4.1	39.5	40.9	5.6	0
Percent of control germination	7.4	91.6	94.9	12.9	0

under the influence of naturally fluctuating temperatures is the best indicator of the response of seeds to temperatures.

No one month is dependably better for germination since the climate varies slightly from year to year. In general, field moisture and temperature conditions favor germination in April and May, and sometimes in September in the central Sierra Nevada (table 2). October and November seeding usually gives good spring germination. Many seeds planted in the open in June, July, or August failed to germinate because of heat damage and rapid drying even when water was added daily. Lack of germination during the winter months is the result of low temperatures and frozen soil.

Absolute temperature limits on germination were not set, but seeds germinated poorly if air temperatures exceeded 33–34°C or fell below —2°C for any appreciable length of time (table 2).

3. Germination and Water (12,000 seeds). To test the influence of water depth and indirectly of oxygen deficiency on germination, one thousand seeds were germinated under each of the following depths of calm water: 0.5, 1.0, 2.0, 3.0, 4.0, 5.0, 10.0, 20.0 cm and under ± 100 cm of flowing water. Seeds were sewn into weighted cheesecloth packets. A similar test was run using one thousand seeds under 30 cm of water aerated by a pump. Water temperatures varied between 11° and 16°C.

The moisture tests were designed to indicate the ability of seeds to germinate under flooding conditions which often occur in the groves in the spring.

Seeds placed under different depths of water were swollen and few began to extend the radicle. None of the seeds under water for 32 or 64 days was able to completely extend the radicle or epicotyl. After 3 months under water, the seeds were covered by fungi and still showed no signs of germinating. Low oxygen tension in the water tests might explain germination failure. But it was not possible to measure directly oxygen availability to seeds under water. Seeds aerated in 30 cm water did not germinate either, although some were able to extend the radicle. No further germination occurred after 3 months of aeration. Eight percent of the seeds removed from aerated water after one month and placed on moist filter paper did germinate proving that these seeds were still alive. Comparable seeds from unaerated water tests were unable to germinate when placed on moist filter paper. Seeds in aerated water appeared to receive enough oxygen to maintain life for a month, but not enough to germinate.

Table 2. Germination of Seeds Under Natural Fluctuating Air Temperatures (°C)—22,000 Seeds.

	1959			1960			1961		
	% Germination	Temp. °C		% Germination	Temp. °C		% Germination	Temp. °C	
		Max.	Min.		Max.	Min.		Max.	Min.
January	—	—		0.0	13	−20	—	—	—
February	0.0	19	0	0.0	21	−18	—	—	—
March	9.8	24	−7.	6.7	21	−10	—	—	—
April	12.7	29	−7.	12.9	28	−10	—	—	—
May	48.5	34	−2.	25.2	34	−11	13.0	37	−1
June	0.0[1]	37	+2.	19.3	37	− 2	10.0	37	+3
July	6.8	35	0	14.0	35	− 5	28.1	35	+2
August	15.4	31	−2.	14.3	34	− 3	—	—	—
September	38.2	31	−3.	36.7	26	− 6	—	—	—
October	—	—	—	—	—	—	—	—	—
November	20.0	25	−10.	0.0	27	− 3	—	—	—
December	0.0	18	−22.	0.0	19	− 3	—	—	—

[1] Failed because of drying. All other tests were kept moist.

There is little chance for *S. giganteum* to become established in areas inundated for more than a month. In the groves, widespread flooding rarely lasts more than a few days, but swamps, creek margins and depressions may remain under water for months.

4. Germination and Light (10,000 seeds). Germination tests used full light (7,000 f.c.), one-half full light (3,500 f.c.), and total darkness from the time of moistening. Light intensities were checked with a G.E. light meter. Temperatures ranged between 14°–16°C. Full light was created by placing the Petri dishes 1 m from a fluorescent light source. For half full light the same source was shaded to half intensity. For total darkness, the seeds were moistened after being placed in a black box in total darkness. Another test exposed the seed in covered dishes to full sunlight (10,000 f.c.) during the day.

Seeds showed 98 to 100% of control germination under half light (artificial) (table 3). When seeds were placed in full sunlight out-of-doors during the summer, the compound effects of heat to 60°C and rapid drying appeared to prevent germination. The influence of high light intensity in the absence of high heat was not studied. Seed germination is retarded and seedlings are etiolated in dark tests, but germination ranged between 64.6 and 75.7% of control germination.

In nature, *S. giganteum* seeds germinate on the litter surface or on mineral soil. Tests show that the litter surface resists wetting and dries quickly producing a poor seed bed. Rarely do the light seeds penetrate to the deeper, moist layers of the litter where germination can occur, but seedling emergence is unlikely because of limited reserve food. Mineral soil in full sunlight often dries too quickly for germination unless the seed is partly buried. Field tests and observations show that the best conditions for germination are disturbed mineral soil in moderate shade.

TABLE 3. PERCENT OF CONTROL GERMINATION UNDER VARIED LIGHT CONDITIONS—10,000 SEEDS

Test No.	Total Darkness 0 f.c.	Half Full Light 3,500 f.c.	Full Light 7,000 f.c.
	Percent of Control		
1	75.7	100.0	0.0
2	64.6	100.0	0.0
3	73.1	98.0	0.0

Etiolation may enable seedlings arising deep in the soil or litter to reach the surface and begin photosynthesis, although etiolated seedlings 10 cm long often fail to recover in full sunlight. The precise location of seeds on the forest floor determines whether germination and growth can occur.

5. Germination and pH (16,000 seeds). Two thousand seeds were germinated in Petri dishes on filter paper moistened with H_2SO_4 and NaOH solutions of the following pH levels: 2, 3, 4, 5, 6, 7, 8, and 9. The acidity of the solution was checked before moistening the filter paper and after 32 days using a Hellige pH kit. No measurable changes in pH occurred during the 32 days, but minor fluctuations probably did occur.

Soil acidity influences seedlings after germination more than seed germination itself. Acid solutions may be beneficial in scarifying the seeds, although scarification is not necessary to germination. At pH 6, germination was 82.6% of that of the controls while germination dropped to 63.3% of controls at pH 9, and 35.7% at pH 2 (table 4, 10°C). Germination was better at all pH levels at 20°C than at 10°C. Seedlings developed under pH 2, 3, and 4 were dwarfed with abnormal, stunted, reddened roots. Swelling developed in the root and root crown regions. Seedlings from seed germinated at pH 5 were slightly abnormal. All other treatments produced normal seedlings except for pH 9 where seedlings were dwarfed and intensely blue-green. Although pH 6 and 7 favor the best germination, soil pH should not limit germination in the groves which range from pH 5.6 to 7.9. The influence of sulfate ions in the solution cannot be overlooked in this test. It was not possible to separate the influence of the H+ ions from that of the sulfate ions.

Studies by Zinke and Crocker (1962) show that soil pH varies from acid at the base of a mature tree to progressively less acid away from the tree. The influence of pH on germination was tested in this study to determine whether variability in soil pH within the groves could limit germination.

6. Age of Seeds and Germination (4,100 seeds). The seeds tested had been stored for 1, 2, 3, 4, and 20 years, at —10° to +10°C. The 20-year-old seed was from a different source than the younger seeds, but its average germination at 1-year was almost identical with that of the 1-year-old seed used in this test. All seeds appeared to be sound, based on cutting a sample lot of seeds and examining the embryo. In these limited tests, seeds decreased in average viability by 32% in 20 years.

Table 4. Percent of Control Germination of Seeds Moistened by Solutions of Different pH Values—16,000 Seeds

	Percent of Control							
	pH							
Temperature	2	3	4	5	6	7	8	9
10°C	35.7	61.2	60.8	70.9	82.6	80.6	78.0	63.3
20°C	—	90.3	92.8	87.2	101.3	102.6	90.5	80.9

7. Depth of Planting and Germination (1,400 seeds). Seeds were planted from 0.2 to 6.2 cm deep at 0.2 cm intervals in mineral soil in a glassfaced frame, and the maximum seed depth allowing successful emergence over a 60-day period was determined.

In mineral soil, seeds can germinate at depths of 6 cm, but beyond about 2.4 to 3.6 cm, few seedlings can reach the surface.

In litter, seeds grow each day into a microenvironment with more light so that they can emerge from greater depths than in soil. Although seedlings endure etiolation to over 10 cm in total darkness, few of these severely etiolated seedlings survive in full light. At 10 cm depth, the litter is usually sufficiently moist for seeds to germinate, but few *S. giganteum* seeds can penetrate to this depth, and chances of seedling emergence are slim.

Tests with seeds of competing species show that larger seeds can penetrate the litter more effectively and produce seedlings which emerge from depths greater than 3.6 cm. *Sequoiadendron giganteum* seeds store a limited amount of food. The seeds of competing species store more reserve food than can *S. giganteum* seeds and can emerge from greater depths in the soil. This inability to germinate on dry surface litter, or to push through deep litter or soil is seriously hampering reproduction of the species which was formerly adapted to periodic fires that reduced litter depths. *Abies concolor* and *Libocedrus decurrens* which have less strict germination requirements are taking over gradually.

Many groves in undisturbed areas have local spots of good *S. giganteum* reproduction usually occurring in openings on slopes and often sites of old windthrows. Microerosion on these slopes tends to wash the seeds into the litter or soil. Many seedlings of all species grow here, but once established, *S. giganteum* can hold its own. Logged and burned groves normally have abundant reproduction (average of 7.3 young *S. giganteum* to each parent stump).

8. Chemical Inhibitors (6,000 seeds). The possible existence of chemical inhibitors in the litter of *S. giganteum* and mixed litter of *Pinus* spp. and *Abies concolor* was tested using water extracts (litter soaked for 24 or 48 hours) on seeds. No evidence of inhibition was found with the concentrations used.

9. Rodent Damage to Seeds and Food Preference. Six major food preference tests were set in the fall of 1960 and in the spring of 1961 in an area in the northern range of the species to determine whether repro-

duction failure is the result of seed-eaters destroying *S. giganteum* seeds. Twenty-four daily trials consisted of groups of 50 seeds, fruits, or cones of common trees. In the early trials, foods were placed in separate piles so that any disturbance was obvious. Later, the foods were mixed in piles so that seed-eaters had to sort through the seeds to locate those preferred. Isolated tests using only *S. giganteum* seeds were also made. The number of seeds removed were counted each day and the supply renewed.

These trials were not conducted in an area where seed-eaters commonly have access to *S. giganteum seeds.* Animals in the groves might react differently from those of adjacent areas. Seed-eaters were identified by periodic observation of feeding stes and trapping. The results were:

Species	*% of food parcels removed*
Libocedrus decurrens	0.1
Abies magnifica	0.3
Juniperus occidentalis	2.0
Sequoiadendron giganteum	3.0
Abies concolor	4.0
Pinus sabiniana	7.0
Quercus kelloggii	35.0
Quercus chrysolepis	36.0
Quercus wislizenii	40.0
Quercus douglasii	62.0
Pinus ponderosa	76.0
Pinus jeffreyi	82.0
Quercus lobata	84.0
Pinus lambertiana	86.0

Not all seeds, cones, and fruits were sound and their removal does not prove that they were eaten. The animals frequently left unsound food parcels of even the most sought-after species.

These results suggest that the small size and low food return of *S. giganteum* seeds or cones makes them undesirable to seed-eaters who prefer pine seed or acorns. In isolated tests using only sound *S. giganteum* seeds, *Peromyscus maniculatus* and *Eutamias speciosus* destroyed a few seeds. Preference for larger food parcels was noted during the fall in the caching period. *Cyanocitta stelleri* (Steller Jays) remove large quantities of acorns and pine seed, but whether these were eaten or not is unknown.

The most undesirable foods are the resinous seeds of *Libocedrus decurrens, Abies concolor, Abies magnifica,* and the cones of *Juniperus occidentalis*. The most desirable food was *Pinus lambertiana.*

The unattractive nature of *S. giganteum* seed argues in favor of a rapid spread of this adaptable species, but deep litter in the absence of fire is preventing its spread.

A. *Seed Size* (2,000 seeds). Exceptionally large sound seeds (8 mm average length) germinated 153% better than sound seeds of mixed sizes. Soundness of seed was determined by cutting through a sample lot of seeds and determining if the seed appeared to be normal. Small apparently sound seeds (under 4 mm average length) germinated only 6.9% as well as the controls.

B. *Germination percent of seeds from 20-year-old trrees* (194 seeds). None of the mature seeds collected from 20-year-old trees in a plantation near Pinecrest, California, germinated, even after stratification. Some of these seeds were not sound. It appears that the species does not produce viable seed at 20 years of age.

C. *Sequoiadendron giganteum cone extract and seed germination* (3,000 seeds). The red material containing gallic acid, pyrogallol, and sugars from the cones is credited with improving germination (Fry and White, 1938). Pigment solutions of 10, 25, 50, 75, and 85% by weight were used to moisten seeds in germination tests.

Cone extract in concentrated dosage (85%) retarded seed germination by one month. This concentration produced smaller seedlings than did the others. The slowing of germination and reduced seedling size may result from osmotic effects since the solution used was supersaturated. No concentration of the extract tested increased seedling size or vigor.

D. *The influence of fire on litter and germination* (6,000 seeds). In burned groves, young seedlings are often abundant. How does litter influence germination? Several hundred grams of litter from the McKinley grove were burned in an oven. Half of the litter was partly burned and the other half was reduced to a fine ash. Germination was tested using partly burned litter and ash dampened with water in Petri dishes. Half of the tests were covered to prevent drying and half were uncovered to the drying effect of air at 10°C. A related experiment using the gravimetric method determined the changes in dry weight and water holding capacity brought about by burning *S. giganteum* litter.

Sequoiadendron giganteum seeds placed on unburned litter exposed to the drying effect of the air did not germinate. The litter resists wetting and will float for some time on water, but the strong tendency for surface drying of the litter is unfavorable to germination. Litter floated on water but covered to reduce surface drying proved to be a good seedbed with 98.3% of control germination. Results on mineral soil indicate that germination parallels that of the filter paper controls as long as the surface is kept moist. Germination on ash was fair (51%) while germination on partially burned litter (covered) was good (98% of control).

Partially burned litter averaged 68% weight loss over unburned litter, but retained an average of 273% more moisture (by weight) than was retained by unburned litter. Burned litter is reduced in volume so that seeds do not have to penetrate deep layers of dry litter. Partly burned litter holds more moisture than unburned litter and seeds landing on the former have a good chance to germinate before it dries. Partial burning appears to increase the water holding capacity of litter by increasing the number of spaces which can retain and give up water easily. Small hygroscopic cells which hold water tenaciously are broken into larger spaces which can take up and give up water more easily than can cellulose walls.

The black, heat absorbent, partly-burned litter should increase surface temperatures in the shaded, cool groves to levels well-suited to germination. Fire in the groves in years past appears to have aided natural reproduction in several ways (Biswell, 1961).

E. *Germination percent of the seeds from 42 groves* (12,000 seeds). Cones containing seeds on the ground were collected from 42 of the groves in 1959. One hundred seeds from each grove were tested for germination in Petri dishes, and another 200 from the same groves were planted in March at 1 cm depth in the soil and covered by litter.

The seeds from these 42 groves averaged 22.5% germination proving that the forest floor has the potential of producing many seedlings, but this potential is not being realized.

DISCUSSION

Sequoiadendron giganteum under natural conditions without fire protection is a long-cycle fire-climax species. Under protection from fire, it appears to be a subclimax species leading to a climax stand dominated by *Abies concolor*. The absence of natural wildfires is threatening the future of the giant sequoia.

The undisturbed *S. giganteum* groves before the advent of white man were adapted to periodic light fires and interims of 7–50 or more years for starting young growth. These light fires cleaned away dead or diseased trees and removed excess litter and debris so that reproduction was possible. Today there are an average of only 1.7 young trees (recent reproduction not yet producing cones) for each mature parent tree in the groves frequented by tourists. This scarcity of reproduction is traceable directly to the accumulation of litter on the forest floor. Where logging has disturbed the litter and exposed bare soil, there are 7.3 young trees to each old parent stump.

The reproductive potential for the species was based on an average of 2,000 cones per tree per year (figuring good and bad cone years) 210 seeds per cone, and an estimated average life span of 3,000 years.

The 1.2 billion seeds estimated per tree in a lifetime is corrected for 66% which are abnormal or are not released from the cones, 25% rodent damage, and 20% average germination. This leaves an estimated 60,000 potential offspring from one tree, more than enough to increase the natural range of the species. But the tree is not increasing its natural range in most places.

We cannot allow destructive wildfires in the Sierra Nevada today because of the threat to human life and property. We must find some means of producing the same conditions which fire used to create if *S. giganteum* is to flourish in nature. Perhaps gentle surface scarification of the forest floor will help to create new seedbeds. Where litter has accumulated to depts of 0.5 to 0.7 m, the only hope appears to be mechanical removal. Any disturbance of the soil must take into account the shallow root system.

SUMMARY

Seed germination tests covered the influence of fluctuating and fixed temperatures, water, light, pH, age, planting depth, and seed-eaters on seed germination of *S. giganteum*. Studies aimed at understanding the failure of the species to reproduce abundantly in nature included the influence of seed size, cone extract, and seedbed conditions on the germination of *S. giganteum* seeds. Results show that:

1. Under fixed temperatures, *S. giganteum* seeds germinate well at 10° and 20°C (39.5 to 40.9%).
2. Germination under natural fluctuating air temperatures is best between —2° and +34°C, provided soil moisture is adequate.
3. Seeds will germinate on moist surfaces but not under water.
4. Seeds germinate best in reduced light (5,000 f.c.).
5. Germination is influenced slightly by pH, but seedling growth from seeds germinated below pH 5 is abnormal. Healthy seedlings and good growth resulted from seeds germinated at pH 6, 7, and 8.
6. *Sequoiadendron giganteum* seeds decreased in viability by 32% in 20 years (limited data).
7. Seedlings seldom reach the surface if seeds are germinated below 2.4 to 3.6 cm in the soil, depending on the degree of compaction.
8. No chemical inhibition of germination by litter extracts or cone extract was found.
9. Larger seeds germinate better than small seeds by as much as 146%.
10. Partially burned litter can hold up to 273% more available water by weight than unburned litter and forms a good seedbed.
11. Seed-eaters prefer the seeds of *Pinus lambertiana* (sugar pine) and the acorns of many oaks to *S. giganteum* seed.
12. The failure of the trees to spread and expand their present range is the result of deep layers of surface-dry litter which make germination and early survival difficult for trees with such small seeds.

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A CYTOTAXONOMIC STUDY OF A NATURAL HYBRID BETWEEN AGROPYRON CRISTATUM AND A. SUBSECUNDUM

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Reports of interspecific hybrids in the Tribe Triticeae of the Gramineae have become commonplace except for those involving diploid *A. cristatum* (L). Gaertn. Grass hybrids involving New World and Old World *Agropyron* are few in number (Dewey, 1967; 1964a; 1964b; (1961). The present paper reports an *A. cristatum* hybrid found by the authors near the United States Forest Service boundary above Mendon, Utah in 1962. Two species of *Agropyron* were closely associated with the hybrid: *A. cristatum* and *A. subsecundum* (Link) Hitchc. Bowden (1965) and some other investigators have accepted the combination *A. trachycaulum* (Link) Malte for this entity and regard *A. subsecundum* as an awned variety of *A. trachycaulum*. No other species of *Agropyron* was found in the area after a careful search. *Elymus glaucus* Buckl. and *Hordeum jubatum* L. were present in the area but not in abundance and not near the hybrid. Specimens of the species and hybrid discussed in this paper are deposited at the Intermountain Herbarium at Utah State University.

Comparative Morphology of Putative Parents and Hybrid. The diploid *A. cristatum* growing within inches of the hybrid had glumes distorted near the base, curved awns, and blades strongly pilose on the ventral surface. These morphololigical characters will usually separate the diploid *A. cristatum* from the tetraploid, *A. desertorum,* where the glumes and awns are straight and the ventral surface of the blades glabrous or only slightly pilose. *Agropyron subsecundum* was typical of the plants found in northern Utah. The single bunch of the hybrid was conspicuous, as it appeared to be intermediate in most characters between the suspected parents.

The hybrid plant as it was found on the mountain produced spikes with solitary spikelets at each node of the rachis but clonal material grown in the field nursery had a tendency to produce two spikelets at a node on the lower part of the spike. *Agropyron subsecundum* and *A. trachycaulum* often do this when grown under optimal ecological conditions. *Agropyron cristatum* produces a single spikelet at each node under all conditions.